FIGURE 1. Flower parts.—A. *Portlandia* (redrawn after Aiello, 1979).—B. *Bikkia* (redrawn after Jérémie & Hallé, 1976).—C. *Chiococca* (redrawn after Correll & Correll, 1982).—D. *Coutarea* (redrawn after Steyermark, 1974). Bar scales = 1 cm.

stema and *Coutarea* (Fig. 1) usually have few large flowers and dry, many-seeded capsules. An affinity between these taxa has never been proposed, and in the latest classification (Robbrecht, 1988) they are placed in different subfamilies, with the Chiococceae in the Antirheoideae and the others in the Cinchonoideae.

The molecular analysis prompted a more detailed morphological analysis of these taxa. I found that they share several specific characters (Table 1, characters 1–7): corolla funnelform or rotate; corolla aestivation imbricate; stamens inserted at the corolla base; filaments fused into a basal ring; anthers linear, basifixed; and stigmas entire or indistinctly lobed. The combination of these characters, particularly the staminal arrangement, is rare in the family, but not unique to these four genera, because they also characterize the subtribe Portlandiinae (*Portlandia*, Fig. 1) of the tribe Condamineeae. In addition, members of the Portlandiinae usually have very large flowers; in the genera *Cubanola*, *Osa*, *Portlandia*, and *Thogsennia*, it is not unusual to have 20-cm-long corollas.

The neotropical genus *Portlandia* and associated taxa (≈ Portlandiinae) have recently been revised by Aiello (1979), who identified the same characters (Table 1, characters 1–7) and indicated that *Exostema*, *Coutarea*, and other genera also have identical character states. Aiello did not reconsider the established tribal classification and did not associate *Exostema* and *Coutarea* with *Portlandia*, because the first two genera have vertically arranged winged seeds, characteristic of the Cinchonoideae, while *Portlandia*, of the tribe Condamineeae, has horizontally arranged wingless seeds. However, the orientation of the ovules to the placentas and the occurrence of a seed wing are

characters that can vary even within the same genus (e.g., in *Steenisia* and *Cinchona*). Because these homoplastic characters have been the main criteria for tribal delimitation in the subfamily Cinchonoideae, it is not surprising that the classification seems arbitrary (see Robbrecht, 1988). The paraphyly of the tribe Cinchoneae was also indicated by the cpDNA analysis (Bremer & Jansen, 1991).

Because the tribal classification is uncertain, it seemed possible that other genera could be closely related to *Portlandia*, *Exostema*, and *Coutarea*. Hence I gathered additional morphological information from most genera of the Chiococceae and the Condamineeae (listed in Robbrecht, 1988), as well as from other genera reported to have the same staminal arrangements (Hooker, 1873; Schumann, 1891). A majority of the genera were studied from herbarium material (in S and UPS), and complementary data were taken from the literature (Mueller, 1861; Hooker, 1873; Schumann, 1891; Verdcourt, 1958; Bremekamp, 1966; Steyermark, 1974; Jérémie & Hallé, 1976; Darwin, 1977; Aiello, 1979; Jansen, 1979; Correll & Correll, 1982; Ridsdale, 1982). The following genera of the tribe Condamineeae (Robbrecht, 1988) were studied but rejected as unrelated to *Portlandia*, *Exostema*, and *Coutarea*, because they lack characters 1–7 listed in Table 1, particularly the staminal characters: *Chimarris*, *Condaminea*, *Flexanthera*, *Kerianthera*, *Parachimarris*, *Picardaea*, *Pinckneya*, *Pogonopus*, *Rustia*, and *Tresanthera*. The following genera of the Chiococceae were also rejected: *Allenanthus*, *Chiona*, and *Hodgkinsonia*. *Allenanthus* and *Chiona* have neither the staminal characters nor the same corolla shape, but they have imbricate aestivation. The flowers of

TABLE 1. Character list. Plesiomorphic state = 0. Apomorphic state = 1 or 2. Character 10 is treated as non-additive and character 12 as additive.

1. Corolla: neither funnel-shaped nor rotate, 0; funnel-shaped or rotate, 1.
2. Aestivation: not imbricate, 0; aestivation imbricate, 1.
3. Stamens; not inserted at the corolla base, 0; inserted at the corolla base, 1.
4. Stamens: not fused, 0; stamens fused into a basal ring, 1.
5. Anthers: not linear, 0; linear, 1.
6. Anthers: dorsifixed, 0; basifixed, 1.
7. Stigma: distinctly lobed, 0; indistinctly bilobed or not, 1.
8. Inflorescence: terminal, 0; axillary, 1.
9. Flowers: not yellowish, 0; often yellowish, 1.
10. Corolla: between 1 and 2 cm, 0; < 1 cm, 1; > 10 cm, 2.
11. Corolla lobes: neither recurved nor reflexed, 0; recurved or reflexed, 1.
12. Corolla lobes: ovate, 0; triangular, 1; linear, 2.
13. Cross section of corolla: circular, 0; distinctly angled, 1.
14. Filaments: glabrous, 0; hairy, 1.
15. Anthers: not exserted, 0; exserted, 1.
16. Stigmatic area: not of two twisted lines, 0; of two twisted lines, 1.
17. Mesocarp: dry, 0; fleshy, 1.
18. Endocarp: not compressed, 0; compressed, 1.
19. Number of seeds per carpel: more than one, 0; one, 1.
20. Seed: not winged, 0; winged, 1.

Hodgkinsonia are very different, with pitcher-shaped corollas, valvate aestivation, short filaments inserted at the midlength of the corollas, dorsifixed anthers, and three to four branched stigmas. The fruit of *Hodgkinsonia* is a drupe with a very hard bilocular endocarp and elongated seeds almost devoid of endosperm. These fruit characters clearly demonstrate that the genus belongs to the tribe Guettardeae, which also was indicated in the original description of the genus (Mueller, 1861). The genus *Phialanthus* has also been excluded since the anthers are ovate and the filaments are free, inserted at the corolla base. I have not been able to study material of the genus *Placocarpa*, but the description (Schumann, 1891) does not indicate any close connection to the *Chiococca* group.

Three genera of uncertain position in the Rubiaceae have been mentioned in connection with the Chiococceae or the Condamineeae (Robbrecht, 1988): *Mastixiodendron* (revised by Darwin, 1977); *Kajewskiella* (revised by Jansen, 1979); and *Pseudomussaenda* (treated and illustrated in Bridson & Verdcourt, 1988). None of these genera
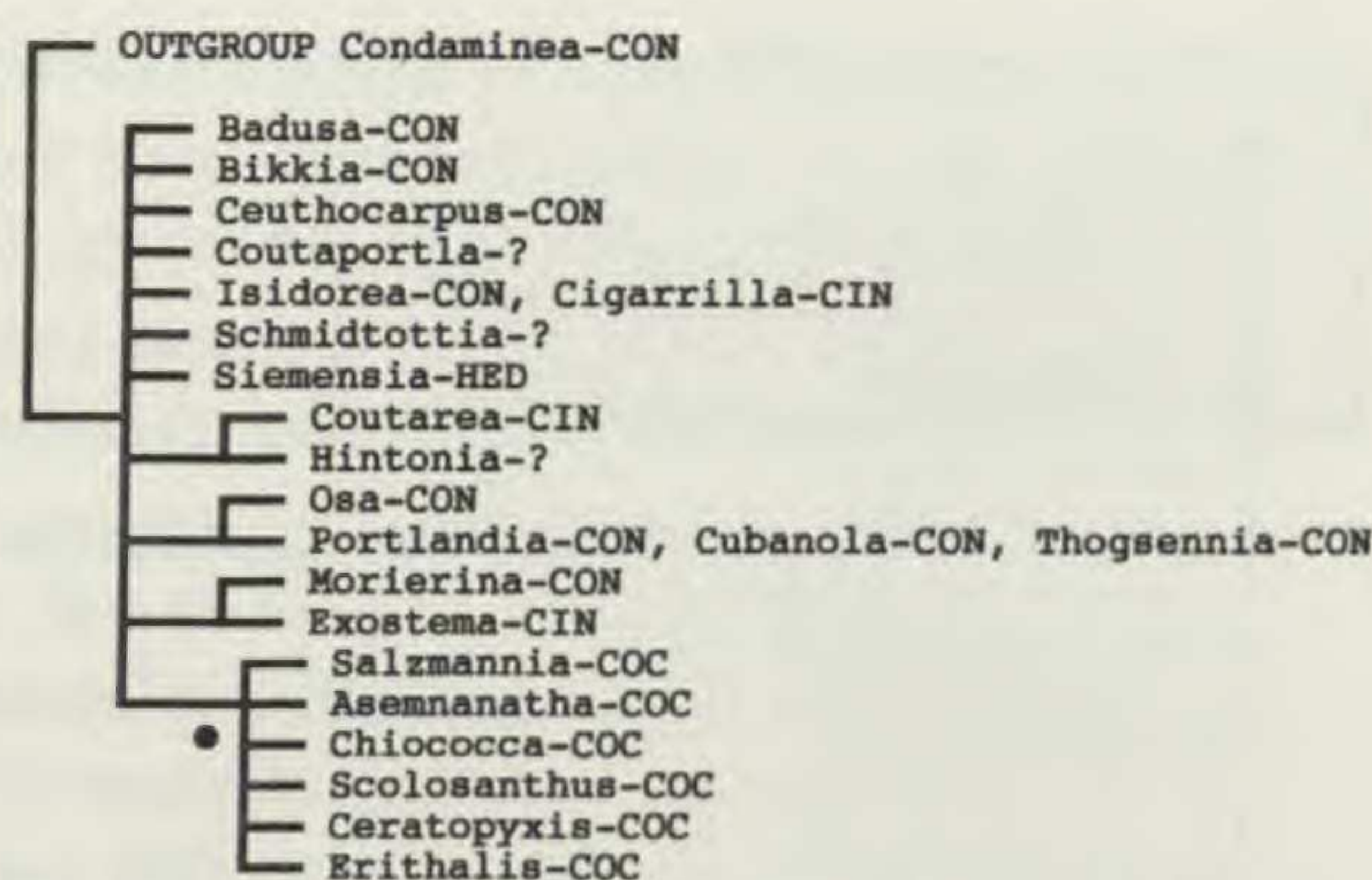

FIGURE 2. A strict consensus tree for 92 equally parsimonious Wagner trees with *Condaminea* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (CIN = Cinchonoideae, CON = Condamineeae, COC = Chiococceae, and HED = Hedyotideae, according to Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

have the characteristic staminal arrangements or stigma shape. In addition, the pollen of *Mastixiodendron* (Darwin, 1977) is tectate, while the pollen of the *Portlandia* group is diffusely foveolate with echinate processes (Aiello, 1979).

All taxa with fused filaments and the combination of characters 1–7 (Table 1) were hypothesized to form a new monophyletic group. A character matrix (Table 2) for these taxa was constructed and analyzed with Wagner parsimony (Hennig86; Farris, 1988). As the sister-group relationships within the family are mostly unknown, four functional Rubiaceae outgroups, representing three tribes, were used: *Condaminea* (Condamineeae), *Luculia* (Cinchoneae), *Rondeletia* (Rondeletieae), and these three together. With *Condaminea* as the outgroup the result was 92 equally parsimonious trees, 34 steps long, with a consistency index of 0.41, and a retention index of 0.71 (Fig. 2). With *Luculia* as the outgroup there were 16 equal-
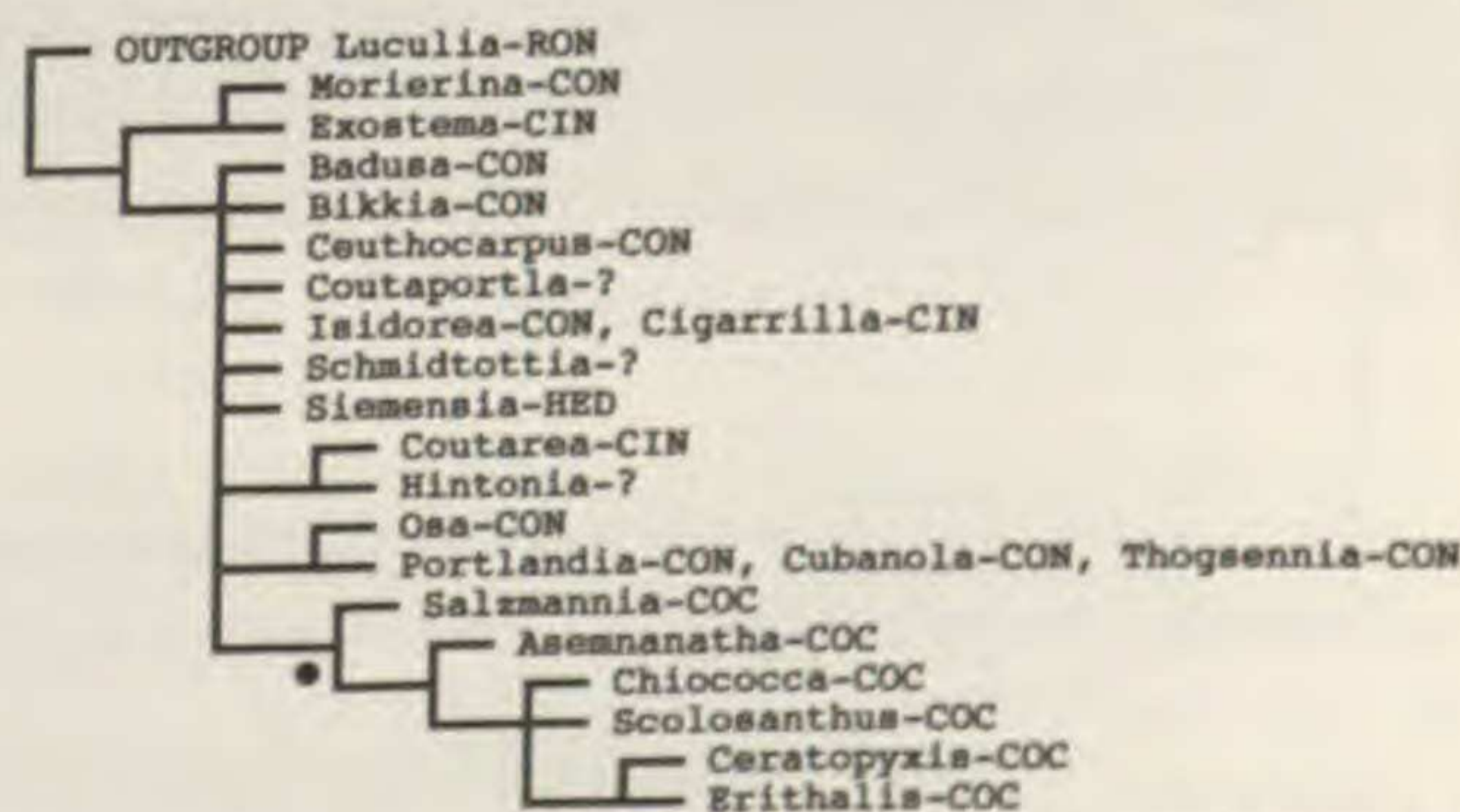

FIGURE 3. A strict consensus tree for 16 equally parsimonious Wagner trees with *Luculia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

```
          OUTGROUP Rondeletia-RON
         ┌── Badusa-CON
         ├── Bikkia-CON
         ├── Ceuthocarpus-CON
         ├── Coutaportla-?
         ├── Isidorea-CON, Cigarrilla-CIN
         ├── Schmidtottia-?
         ├── Siemensia-HED
      ┌──┤  ┌── Coutarea-CIN
         │  └── Hintonia-?
         │  ┌── Osa-CON
         │  ├── Portlandia-CON, Cubanola-CON, Thogsennia-CON
         │  ┌── Morierina-CON
         │  └── Exostema-CIN
         ├── Salzmannia-COC
         ├── Asemnanatha-COC
         ├── Chiococca-COC
         ├── Scolosanthus-COC
         ├── Ceratopyxis-COC
         └── Erithalis-COC
```
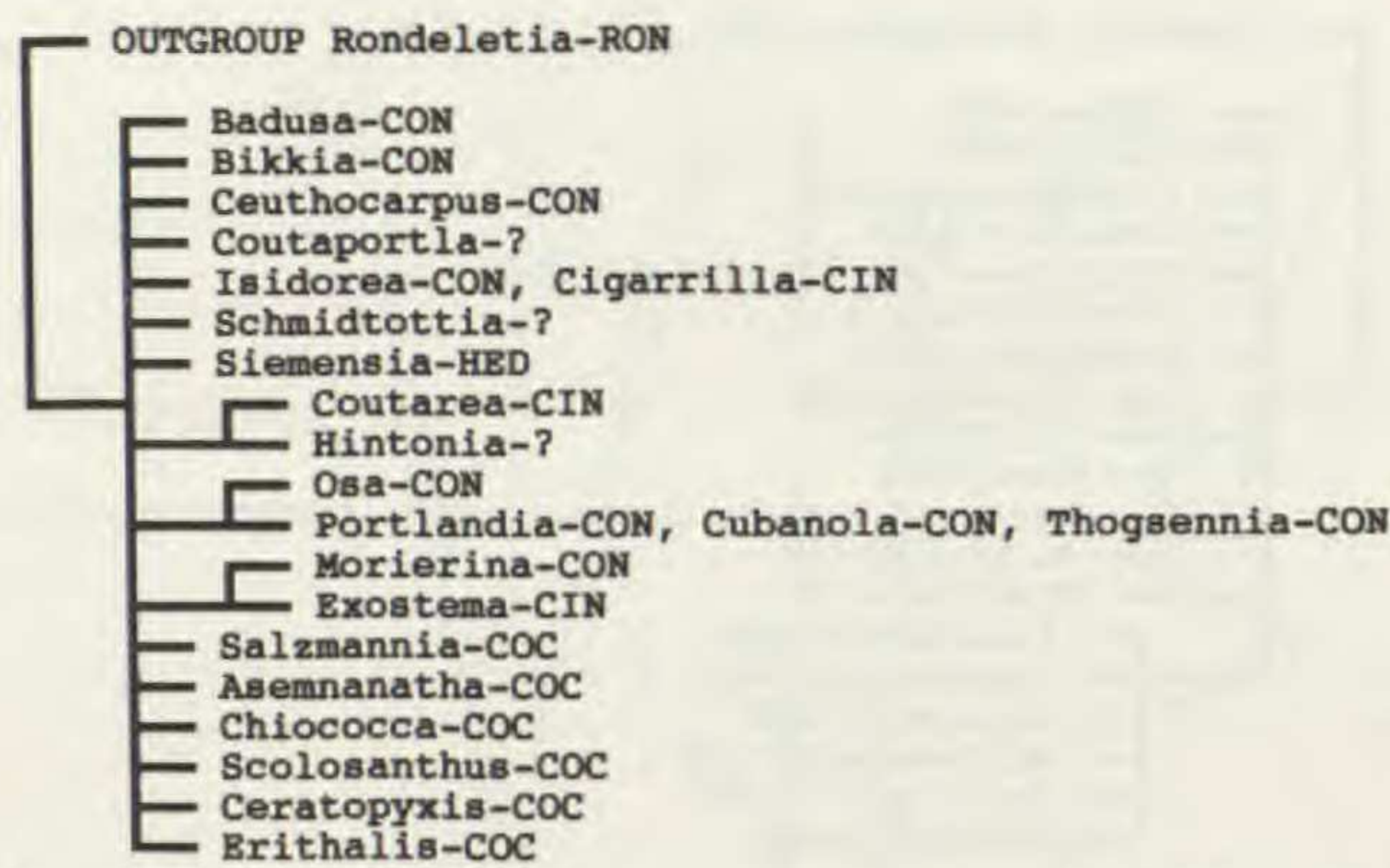
FIGURE 4. A strict consensus tree for 17 equally parsimonious Wagner trees with *Rondeletia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position.

ly parsimonious trees, 35 steps long, with a consistency index of 0.42, and a retention index of 0.71 (Fig. 3). With *Rondeletia* there were 17 equally parsimonious trees, 34 steps long, with a consistency index of 0.44 and a retention index of 0.72 (Fig. 4). When all three genera were used as the outgroup, the result was 58 equally parsimonious trees, 37 steps long, with a consistency index of 0.40, and a retention index of 0.71 (Fig. 5). Most relationships within the ingroup remain unresolved or uncertain, because of the lack of available characters. There were only 13 phylogenetically informative characters and 22 ingroup taxa. However, all genera with small flowers and one-seeded carpels (≈ Chiococceae sensu Hooker f.) were shown to form a monophyletic group (indicated by a dot in Figs. 2, 3, 5) in all analyses except that with *Rondeletia* as the outgroup. This small-flowered group is supported by several flower and fruit characters (Tables 1, 2). If we retain Chiococceae in the narrow sense, all the remaining

```
        ┌── OUTGROUP Condaminea-CON
      ┌─┤── OUTGROUP Luculia-CIN
      │ └── OUTGROUP Rondeletia-RON
      │
      ├── Badusa-CON
      │  ┌── Morierina-CON
      │ ┌┤── Exostema-CIN
      │ │└── Bikkia-CON
      │ │   ┌── Ceuthocarpus-CON
      │ │   ├── Coutaportla-?
      ├─┤   ├── Isidorea-CON, Cigarrilla-CIN
      │ │   ├── Schmidtottia-?
      │ │   ├── Siemensia-HED
      │ │      ┌── Coutarea-CIN
      │ │      └── Hintonia-?
      │ │      ┌── Osa-CON
      │ │      └── Portlandia-CON, Cubanola-CON, Thogsennia-CON
      │ ┌── Salzmannia-COC
      └●┤  ┌── Asemnanatha-COC
        │  ├── Chiococca-COC
        └──┤── Scolosanthus-COC
           │  ┌── Ceratopyxis-COC
           └──┴── Erithalis-COC
```
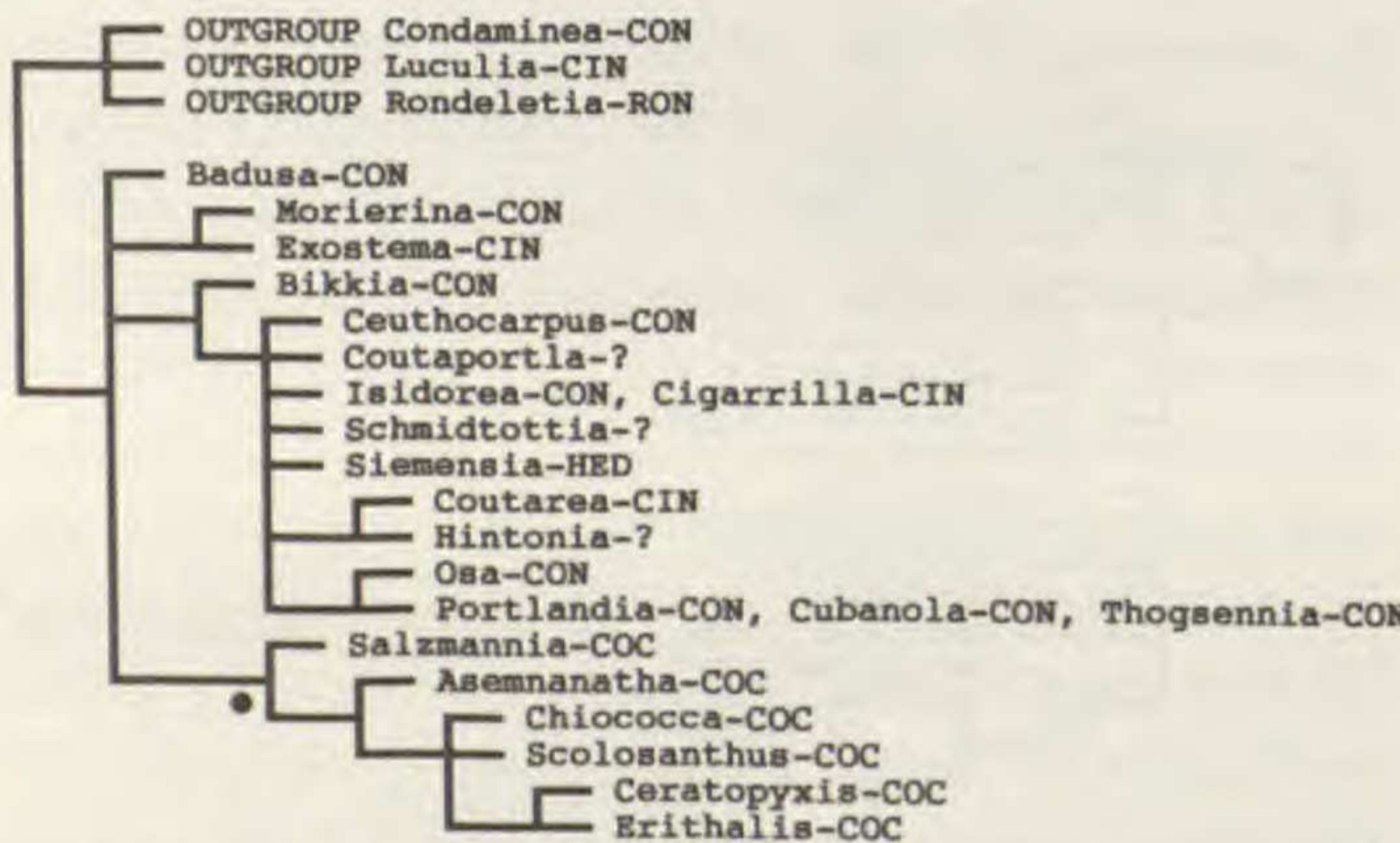
FIGURE 5. A strict consensus tree for 48 equally parsimonious Wagner trees with *Condaminea*, *Luculia* and *Rondeletia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

TABLE 2. Data matrix of 20 morphological characters. Characters 1–7 are synapomorphies defining the study group and not included in the Wagner parsimony analyses. Character numbers are the same as in Table 1. *Condaminea*—CON, *Luculia*—CIN, *Rondeletia*—RON, as well as all three together were used as outgroups. A question mark indicates an unknown or variable state.

		Character number	
		1	2
		1234567	8901234567890
1	*Condaminea*	0000000	0000100100000
2	*Luculia*	0100000	0000000000001
3	*Rondeletia*	0100000	1000000000000
4	*Asemnanatha*	1111111	1111101001010
5	*Ceratopyxis*	1111101	0111101100110
6	*Chiococca*	1111111	1111111001110
7	*Erithalis*	1111111	0011101101110
8	*Salzmannia*	1111111	1?10100001?10
9	*Scolosanthus*	1111111	1111101001110
10	*Badusa*	1111111	1?0010100000?
11	*Bikkia*	1111111	1000111000000
12	*Ceuthocarpus*	1111111	00001?1110000
13	*Cigarrilla*	1111111	1000111010000
14	*Cubanola*	1111111	1020111010000
15	*Coutaportla*	1111111	0000111010100
16	*Coutarea*	1111111	1000111110101
17	*Hintonia*	1111111	1000111110001
18	*Isidorea*	1111111	1000111010000
19	*Morierina*	1?11111	00212?1100001
20	*Osa*	1111111	1020110010000
21	*Portlandia*	1111111	1020111010000
22	*Schmidtottia*	1111111	0100111010000
23	*Siemensia*	1111111	0000111010000
24	*Thogsennia*	1111111	1020111010000
25	*Exostema*	1111111	?101200100001

taxa considered in this analysis (≈ Portlandiinae) become a paraphyletic cluster; so far, no single character has been found to unite the remaining taxa. The best solution to this taxonomic problem is to redefine and widen the tribe Chiococceae, as follows.

Chiococceae J. D. Hooker, Gen. Pl.: 9, 21. 1873.
  Portlandiinae J. D. Hooker, Gen. Pl: 12. 1873, as "Portlandieae." Type genus: *Chiococca* P. Browne.

The tribe Chiococceae is characterized by funnelform or rotate corollas, imbricate aestivation, stamens inserted at the corolla base, filaments mostly villous and fused into a basal ring, anthers linear and mostly basifixed, stigma entire, carpels one- or many-seeded, and fruits drupes or capsules. The included genera are *Asemnanatha*, *Badu-*

sa, *Bikkia* (Fig. 1), *Ceratopyxis, Ceuthocarpus, Chiococca* (Fig. 1), *Cigarrilla, Coutaportla, Coutarea* (Fig. 1), *Cubanola, Erithalis, Exostema, Hintonia, Isidorea, Morierina, Osa, Portlandia* (Fig. 1), *Salzmannia, Schmidtottia, Scolosanthus, Siemensia,* and *Thogsennia.*

PHYLOGENETIC ASPECTS OF SEED DISPERSAL

The Rubiaceae display a wide array of seed-dispersal mechanisms (Bremer & Eriksson, 1992). By making outgroup comparisons with different parts of the Loganiaceae, it can be inferred that the ancestral, plesiomorphic fruit condition in the family is likely to be a many-seeded capsule (Bremer & Struwe, unpublished data). This condition has been altered several times in relation to various dispersal agents, both biotic and abiotic. Adaptations for wind dispersal, in the form of winged seeds or pterophyll, occur in many genera. Bird- and mammal-dispersed fleshy fruits are also common in the family. These are basically of three kinds: drupes, berries, and "*Gardenia*-fruits." The "*Gardenia*-fruits" are characterized by a fleshy to leathery or fibrous to woody mesocarp, covering a juicy or fleshy pulp of placental origin (Robbrecht & Puff, 1986). Berries are the predominant fruit type in the tribe Iserteae. Drupes dominate in the Psychotrieae and Guettardeae. The subfamily Ixoroideae has the most variable array of fleshy fruits; in addition to "*Gardenia*-fruits," which occur solely in this subfamily, drupes and berries are common. The great variety of fruits in the Rubiaceae makes this family particularly suitable for comparative studies of the evolution of dispersal systems. Ecological considerations of seed-dispersal evolution have to a large extent focused on coevolutionary relationships between fruit characters and dispersal agents. The "traditional view" of a close adaptative association between plants and animals has recently been challenged (e.g., Howe, 1984, 1986; Herrera, 1986; Wheelwright, 1988). A persistent problem for evaluation of "coevolutionary" hypotheses is the scarcity of phylogenetic studies of fruit evolution incorporating taxa above the genus level. Until recently only a few such studies had been performed (e.g., Tiffney, 1986; Raven, 1988; Stone, 1989). In order to provide some insight into this research field, Bremer and Eriksson (1992) analyzed fruit evolution in the Rubiaceae. The study was based on the phylogenetic relationships of the family derived from cladistic analysis of cpDNA variation (Bremer & Jansen, 1991). The principal results indicated that fleshy fruits, adapted to animal dispersal, have originated only

a limited number of times (approximately 12), and that they evolved mostly during a period from Eocene to Miocene. The inferences on when fleshy fruits appeared were made indirectly from information on pollen fossils (Bremer & Eriksson, 1992). Moreover, optimization of the fleshy fruit character on the cladogram implied that fruit structure in general has remained unchanged since that period. The analysis rested on two assumptions: that capsules with many seeds do not evolve from other fruit types and that seed number reduction is a "fixed" condition. Given these assumptions, the origin events were positioned in the phylogenetic tree on the lowest (oldest) possible branch that was allowed. Since the time of origin of the different fruit types, thousands of species have evolved; there are now ca. 7,000 extant species with fleshy fruits. These results indicate that specific adaptive interpretations of animal-dispersal modes based on contemporary ecological conditions are unwarranted. In contrast to the fleshy fruits, optimization of the wind dispersal by winged seed character on the cladogram suggested a much less conservative evolutionary pattern. Wind-dispersal adaptations may have been changed repeatedly during the course of evolution in several lineages.

Another issue, much debated in recent years, is how ecological features influence taxonomic diversification patterns (e.g., Stanley, 1979, 1989; Kitchell, 1985). For angiosperms, the prevalent view is that aspects of reproduction and dispersal have been responsible for the tremendous diversification of this group since Late Cretaceous (Raven, 1977; Burger, 1981; Stebbins, 1981; Crepet, 1984). One of several hypotheses of angiosperm diversification states that animal dispersal promotes species richness (Regal, 1977; Tiffney, 1984, 1986). Herrera (1989) tested this hypothesis and concluded that it was inconsistent with data on species number in relation to dispersal modes in both angiosperms and "gymnosperms." This conclusion was, however, not based on explicit phylogenetic inferences; since extant species number is directly correlated to diversification rate only if compared taxa are of equal age (cf. Mitter et al., 1988), the conclusion is difficult to evaluate. Eriksson & Bremer (1991) investigated the "animal dispersal hypothesis" in closer detail for the Rubiaceae. We found no consistent support for the hypothesis, but we did find evidence suggesting a positive association between dispersal ability and species diversification. In shrubs, fleshy fruits are likely to enhance seed dispersal, whereas abiotic dispersal modes are more efficient seed dispersers among herbaceous life forms (Eriksson & Bremer,

1991). These two life form/dispersal mode categories were both comparatively species-rich. This conclusion was robust since it was founded on generic and sister-group comparisons. Hence, this study indicated that diversification patterns are influenced by a combination of features. Future hypotheses should be based preferably on several life cycle characteristics, instead of single features.

The use of phylogenetic approaches in ecology has been considered by several authors (e.g., Ridley, 1983; Felsenstein, 1985; Donoghue, 1989; Funk & Brooks, 1990; Wanntorp et al., 1990; Brooks & McLennan, 1991), but empirical studies in botany are still scarce. A synthesis of ecology and phylogenetic inferences based on molecular and morphological data is a promising field for research. As the research on Rubiaceae has shown, data, hypotheses, and conclusions from molecular and morphological phylogeny and ecology, when considered together, have provided new insights that scarcely had been revealed by studies of ecological, morphological, or molecular data in isolation.

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CIRCUMSCRIPTION AND PHYLOGENY OF THE CAMPANULALES[1]

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ABSTRACT

Systematic relationships of the Campanulales were reexamined through the integration of data accumulated from morphological, anatomical, embryological, palynological, cytological, ultrastructural, chemical, molecular, and paleontological studies. Interpretation of these data suggests that the most natural circumscription of the order may be achieved by retaining Asteraceae and Calyceraceae, adding Menyanthaceae, removing Donatiaceae and Stylidiaceae to Ericales, and including *Brunonia* in Goodeniaceae rather than its own family. Phylogenies based on chloroplast DNA restriction fragment analysis and *rbc*L sequencing, supported by embryological and chemical data, suggest a basal dichotomy into two clades. The first (Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae) has multinucleate tapetal cells, lacks endosperm haustoria, and produces deterrent chemicals (either seco-iridoids or sesquiterpene lactones, but not both) via the mevalonate pathway. The second (Campanulaceae, Cyphiaceae, Lobeliaceae, Sphenocleaceae, and Pentaphragmataceae) has binucleate tapetal cells and terminal endosperm haustoria, but cannot synthesize deterrent chemicals via the mevalonate pathway. Numerous characteristic morphological features (e.g., epigyny, zygomorphy, secondary pollen presentation, uniovulate ovaries) appear to have had multiple origins within the order, vitiating their use as synapomorphies. The order originated no later than the Oligocene, very near the base of the Asteridae, probably in the Cornales–Saxifragales complex.

The Campanulales are an angiosperm order of vacillating circumscription (Wagenitz, 1977). Comparison of current classifications reveals major disagreements on its constituency, the relationships among its constituents, and its relationships to other orders. Possible relationships to the Asteraceae have been of special interest for many years (Greene, 1904; Small, 1919; Leonhardt, 1949; Turner, 1977; Bremer, 1987). In this review, three questions are posed: (1) What is the most natural circumscription of Campanulales? (2) What are the relationships among its component families? (3) To what other orders are the Campanulales related?

OVERVIEW OF CURRENT CLASSIFICATIONS

A complete taxonomic history of the order, which dates at least to Lindley (1833), is not presented here. The discussion is limited to the five major systems in current use: the most recent version of the traditional Englerian classification (Wagenitz, 1964) and the Besseyan classifications referred to as the "Big Four" (i.e., the systems of Cronquist, Dahlgren, Takhtajan, and Thorne). The sequence in which these classifications are discussed reflects a progressively narrower circumscription of Campanulales.

WAGENITZ

The broadest circumscription of Campanulales is that of Wagenitz (1964), who included the following families: Campanulaceae (subfamilies Campanuloideae, Cyphioideae, and Lobelioideae), Sphenocleaceae, Pentaphragmataceae, Goodeniaceae, Brunoniaceae, Stylidiaceae (subfamilies Donatioideae and Stylidioideae), Calyceraceae, and Asteraceae (subfamilies Asteroideae and Cichorioideae). The order was assigned to the dicotyledonous subclass Sympetalae and characterized largely as follows: herbaceous plants (rarely woody), storing carbohydrate as inulin; leaves exstipulate; flowers tetracyclic; corolla sympetalous, pentamerous; androecium isomerous (rarely oligomerous),

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with introrse (rarely extrorse) dithecal anthers, and often with specialized adaptations for secondary pollen presentation; gynoecium oligomerous, inferior (rarely superior), with 1–3(–5) locules, 1(–3) styles, and 1–many anatropous, unitegmic, tenuinucellate ovules.

TAKHTAJAN

The classification proposed by Takhtajan (1980, 1983) differs primarily in the removal of Asteraceae and Calyceraceae to monofamilial orders. Nonetheless, a close relationship was maintained by grouping these three orders as the Asteranae. This superorder is one of several in Asteridae, a subclass essentially identical to the Sympetalae of Wagenitz. The only other differences from the system of Wagenitz involved rank: Brunoniaceae, Pentaphragmataceae, and Sphenocleaceae were demoted to subfamilies (the first under Goodeniaceae, the last two under Campanulaceae), while the Donatioideae were promoted to familial rank. Additional taxonomic structure was provided by grouping the families into two suborders, Campanulineae (Campanulaceae, Donatiaceae, Stylidiaceae) and Goodeniineae (Goodeniaceae).

Takhtajan excluded Asteraceae and Calyceraceae primarily on morphological grounds, although anatomical, embryological, and palynological differences were also cited. Their removal tightened up the morphological characterization of Campanulales by removing families with involucrate capitulate inflorescences, 1-loculed ovaries, and solitary ovules.

In Takhtajan's (1987) recent revision of his system, the treatment of Campanulales at first appears very different. The subfamilies of Campanulaceae have been elevated to familial rank as Pentaphragmataceae, Sphenocleaceae, Campanulaceae, Cyphiaceae, Nemacladaceae, Lobeliaceae, and Cyphocarpaceae (Nemacladaceae and Cyphocarpaceae were segregated from Cyphioideae). The remainder of the Campanulineae formed the new order Stylidiales, while the Goodeniineae were raised to ordinal rank as Goodeniales (with Brunonioideae elevated to familial rank). These three orders, together with Calycerales and Asterales, constitute a smaller subclass Asteridae; the remainder of the sympetalous orders are assigned to a new subclass Lamiidae. The only real difference, however, is an across-the-board inflation in rank; the taxa that constituted a family in the earlier version now make up an order, and what was formerly an order or superorder is now a subclass. The relationships expressed are essentially unaltered from the earlier system, or from that of Wagenitz.

CRONQUIST

The system of Cronquist (1981, 1987a) resembles Takhtajan's original classification in its removal of Calyceraceae and Asteraceae to monofamilial orders, but differs in its complete dissociation of these orders from any relationship with the Campanulales. Instead, Calycerales were allied to Dipsacales, and Asterales to Rubiales. Brunonioideae, Pentaphragmatoideae, and Sphenocleoideae were restored to familial status, while the Cyphioideae, a small group of "transitional" genera connecting Campanuloideae and Lobelioideae, were not recognized formally.

THORNE

A conspicuous difference in the system of Thorne (1968, 1976, 1977, 1981, 1983) is the division of the angiosperms into numerous superorders rather than a few subclasses. Like Cronquist, he completely dissociated Asteraceae and Calyceraceae from Campanulales; the latter family, however, was assigned to Dipsacales rather than to its own order. The Campanulales were reduced further by the removal of Donatiaceae and Stylidiaceae. This action left only Pentaphragmataceae, Campanulaceae (subfamilies Campanuloideae, Cyphioideae, Lobelioideae, and Sphenocleoideae), and Goodeniaceae (subfamilies Brunonioideae and Goodenioideae) in the order.

In justifying the exclusion of Donatiaceae and Stylidiaceae, Thorne (1976: 81) stated that they "have no basic relationships" to the remainder of the order. Rather, they "seem closely related to the Saxifragaceae but are more specialized in various ways" (Thorne, 1976: 89), a conclusion that resulted in their assignment to Rosales suborder Saxifragineae. Their exclusion narrowed the morphological characterization of the order by removing families with less than five stamens, filaments adnate to the style, and distinct styles.

Originally (Thorne, 1968, 1976), the Campanulales were assigned to the superorder Malviflorae, together with Euphorbiales, Malvales, Rhamnales, Solanales, and Urticales. Subsequently (Thorne, 1981, 1983), Campanulales and Solanales were segregated as the Solaniflorae. In both versions, the Asterales were placed in the monofamilial superorder Asteriflorae, Dipsacales in Corniflorae, and Rosales in Rosiflorae.

DAHLGREN

Like Thorne, Dahlgren (1975a, 1977, 1980, 1983; Dahlgren et al., 1981) fragmented Takh-